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Does Physical Protection of Soil Organic Matter Attenuate Temperature Sensitivity?

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Global climate change may induce accelerated soil organic matter (SOM) decomposition through increased soil temperature, and thus impact the C balance in soils. We hypothesized that compartmentalization of substrates and decomposers in the soil matrix would decrease SOM sensitivity to temperature. We tested our hypothesis with three short-term laboratory incubations with differing physical protection treatments conducted at different temperatures. Overall, CO_2 efflux increased with temperature, but responses among physical protection treatments were not consistently different. Similar respiration quotient (Q_{10}) values across physical protection treatments did not support our original hypothesis that the largest Q_{10} values would be observed in the treatment with the least physical protection. Compartmentalization of substrates and decomposers is known to reduce the decomposability of otherwise labile material, but the hypothesized attenuation of temperature sensitivity was not detected, and thus the sensitivity is probably driven by the thermodynamics of biochemical reactions as expressed by Arrhenius-type equations.

Abbreviations: SOM, soil organic matter.

Soil organic matter decomposition, and the resultant CO_2 respiration, is a crucial part of the global C cycle, as it has a significant impact on atmospheric CO_2 levels. Global climate change may induce an acceleration of SOM decomposition through increased soil temperature, and thus significantly impact the C balance in soils (Davidson and Janssens, 2006). Intensive study, however, has revealed variability in the response of soil respiration to temperature and spurned much debate in the literature (e.g., Davidson et al., 2006; Fang et al., 2006; Kirschbaum, 2006; Reichstein et al., 2005). Soil organic matter decomposition has often been described as a set of exclusively biochemical processes, and thus the temperature sensitivity relationships developed by Arrhenius and van't Hoff in the late 19th century have been applied extensively to soil respiration (e.g., Lloyd and Taylor, 1994). It is well established, however, that SOM is not stabilized in soils exclusively by biochemical recalcitrance (Marschner et al., 2008). While the temperature sensitivity of SOM stabilized by biochemical recalcitrance or sorption reactions to mineral surfaces might logically be subject to temperature sensitivities based on the thermodynamics of sorption and enzymatic reactions (e.g., Bosatta and Ågren, 1999), the temperature sensitivity of physically protected SOM is less obvious and has not been tested. Physical protection by occlusion of SOM within aggregates and compartmentalization of substrates and decomposers prevents the substrate from coming into contact with organisms and enzymes. Under conditions where substrate and decomposer are physically separated, there is little to suggest that increased temperatures might increase decomposition. Consequently, the applicability of biochemically based models of temperature sensitivity (i.e., Q_{10}) in the case of a large contribution of compartmentalization by aggregation may be weak.

The temperature sensitivity of SOM decomposition in response to variations in compartmentalization by soil aggregation has not previously been investigated and is the purpose of the current study. The hypothesis we proposed was that increased compartmentalization of substrate and degrader by increased soil aggregation would decrease SOM sensitivity to temperature, evidenced by smaller Q_{10} values in soils with greater physical protection. Three separate short-term laboratory incubations were performed to test the relationship between the temperature sensitivity of soil respiration and physical protection by either disrupting compartmentalization imparted by soil aggregation (Exp. 1 and 2) or by creating contrasting degrees of compartmentalization (Exp. 3). Our hypothesis was tested using whole soil subjected to three degrees of physical disruption (Exp. 1), isolated macroaggregates subjected to physical disruption (Exp. 2), and the location of organic substrate in reconstituted macroaggregates (Exp. 3). In Exp. 2, we also tested whether increased CO_2 efflux with increased temperature was caused by either an increased microbial biomass or greater respiration by an unchanged biomass.

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MATERIALS AND METHODS

Sites and Sampling

Soil was collected in July of 2006 and 2007 from the Russell Larson Agricultural Research Center of Pennsylvania State University in Rock Springs, PA (40°43′ N, 77°56′ W). The soil is a Hagerstown silt loam (a fine, mixed, semiactive, mesic Typic Hapludalf), with a textural composition of 160 g kg^{-1} sand, 670 g kg^{-1} silt, and 170 g kg^{-1} clay in the top 10 cm, and a total organic C concentration of 19.3 g C kg^{-1} soil. The area of sampling is an abandoned pasture that has been under orchard grass (*Dactylis glomerata* L.) for 8 to 10 yr, with no tillage or fertilization occurring during this period. Mean annual precipitation for the area is 975 mm, and mean annual temperature is 9.7°C. Forty-eight soil cores (5-cm height and diameter) were collected from the field, and a 5-kg block of soil (∼10-cm depth) was also collected using a shovel. The field-moist block of soil was first broken apart by hand to pass through a 4-mm sieve and then air dried. The intact cores were also allowed to air dry after some cores were sacrificed for field moisture content and bulk density determinations.

Experiment 1: Incubation of Soil Core Materials

The collected soil cores were divided into three groups to generate three physical protection treatments for laboratory incubation: one-third of the cores were unaltered and retained as intact, one-third were sieved (<2 mm), and the final one-third were subjected to crushing (<75 μm) by mortar and pestle. Laboratory incubations were performed in constant-temperature incubators set to 15, 25, or 35°C. Sieved (∼100 g air-dry soil) and crushed samples (∼85 g air-dry soil) were poured into 125-mL plastic specimen cups and tapped down to maximize bulk density, making it similar to that observed in the field (1.1–1.3 g cm^{-3}). Intact soil cores (∼150 g air-dry soil) were kept in their metal sampling rings and water was added slowly to each sample to achieve ∼55% water-filled pore space based on bulk density and total porosity determinations. Four replicates from each physical protection treatment underwent 1 wk of preincubation, and respiration measurements were subsequently taken daily for 15 d. Samples were incubated in sealed 1-L canning jars containing a 10-mL vial of water to minimize evaporation of water from the soil. The headspace of each jar was sampled using a syringe through a septum installed in the jar lids, and CO_2 concentrations were determined using a LICOR 7000 infrared gas analyzer (LICOR Corp., Lincoln, NE). Jars were aerated every 3 to 4 d to prevent anoxic conditions and CO_2 inhibition by opening the lids, blowing air across the opening using an electric fan for 1 min, and immediately resampling.

Experiment 2: Incubation of Isolated Macroaggregates

The air-dried <4-mm bulk soil was dry sieved by hand on a stack of a 4-mm sieve over a 2-mm sieve. The material remaining on the 2-mm screen was retained as intact 2- to 4-mm macroaggregates, while the material that passed through the 2-mm screen was discarded. A portion of the 2- to 4-mm macroaggregates was then crushed to pass a 500-μm sieve. Four replicates (∼100 g air dry) from each of the intact and crushed macroaggregate samples were prepared for incubation at 15, 25, or 35°C as described above. Samples underwent 1 wk of preincubation and respiration measurements were subsequently taken for 14 d.

After the 25 and 35°C incubations (samples from the 15°C incubation were inadvertently destroyed), samples were analyzed for microbial biomass C and N using the fumigation–direct extraction technique (Vance et al., 1987). Specific respiration was determined by dividing the amount of CO_2 respired during the 2-wk incubations by the amount of microbial biomass C measured at the end of the same period (Anderson and Domsch, 1985; Santruckova and Straskraba, 1991).

Experiment 3: Incubation of Reconstituted Macroaggregates

Reconstituted macroaggregates were prepared in a manner similar to Bartlett and Doner (1988) by dispersing the sampled bulk soil in a 2:1 soil/water paste, which was allowed to dry until the soil was most friable (generally 23% moisture by mass). The partially dried paste was broken up by hand over a sieve stack to isolate the 2- to 4-mm macroaggregates. Two compartmentalization treatments were prepared: (i) ^{13}C-enriched wheat (*Triticum aestivum* L.) residue located *inside* reconstituted macroaggregates by adding the residue (<150-μm particle size) to the 2:1 paste at a rate of 1.7 g straw kg^{-1} soil, and (ii) ^{13}C-enriched wheat residue located *outside* macroaggregates by adding an equivalent amount of residue to air-dry reconstituted aggregates. Reconstituted macroaggregates with no added residue were used as a control. Analysis of the $\delta^{13}C$ signatures of several individual aggregates presumed to contain the ^{13}C-enriched wheat straw confirmed the presence of the label (data not shown). Four replicates (∼50 g air dry) of each treatment were prepared for incubation at 25 or 35°C as described above. Samples underwent 1 wk of preincubation and respiration measurements were subsequently taken for 30 d.

Analyses of the isotopic signature of the respired CO_2 ($\delta^{13}CO_2$) were performed after 2, 9, and 30 d of incubation by injection of 250 μL of headspace gas into a Thermo TRACE-GC gas chromatograph (Thermo Fisher Scientific, Waltham, MA) equipped with a Varian Poroband-Q 25-m column (Varian Inc., Palo Alto, CA), coupled to a Thermo-Finnigan Delta+ isotope ratio mass spectrometer. The proportion of respired CO_2 derived from the labeled residue was determined using a standard mixing model where endpoint $\delta^{13}C$ signatures were 721.6 ± 4.8‰ (mean ± standard deviation) for the ^{13}C-enriched wheat straw and −23.6 ± 0.8‰ for respiration from the unamended soil.

Temperature Sensitivity

The temperature sensitivity of SOM dynamics during these short incubations is expressed using respiration quotients (Q_{10}), which were determined by plotting the log of the cumulative respiration (because of the exponential relationship between temperature and respiration [e.g., Lloyd and Taylor, 1994]) as a function of incubation temperature for each replicate. The equation for the best-fitting linear regression for each treatment was then used to estimate the cumulative respiration at 25 and 35°C. The value of Q_{10} was determined by dividing regression-based estimates for cumulative CO_2 respired at the higher temperature by the estimate for cumulative CO_2 respired at the lower temperature.

Statistical Analyses

Experimental data were analyzed using two-way ANOVA procedures with SigmaStat (Systat Software Inc., Point Richmond, CA), with physical protection treatment and incubation temperature as the two main factors in the model. Separation of means was tested on significant main factors using Tukey's significant difference test.

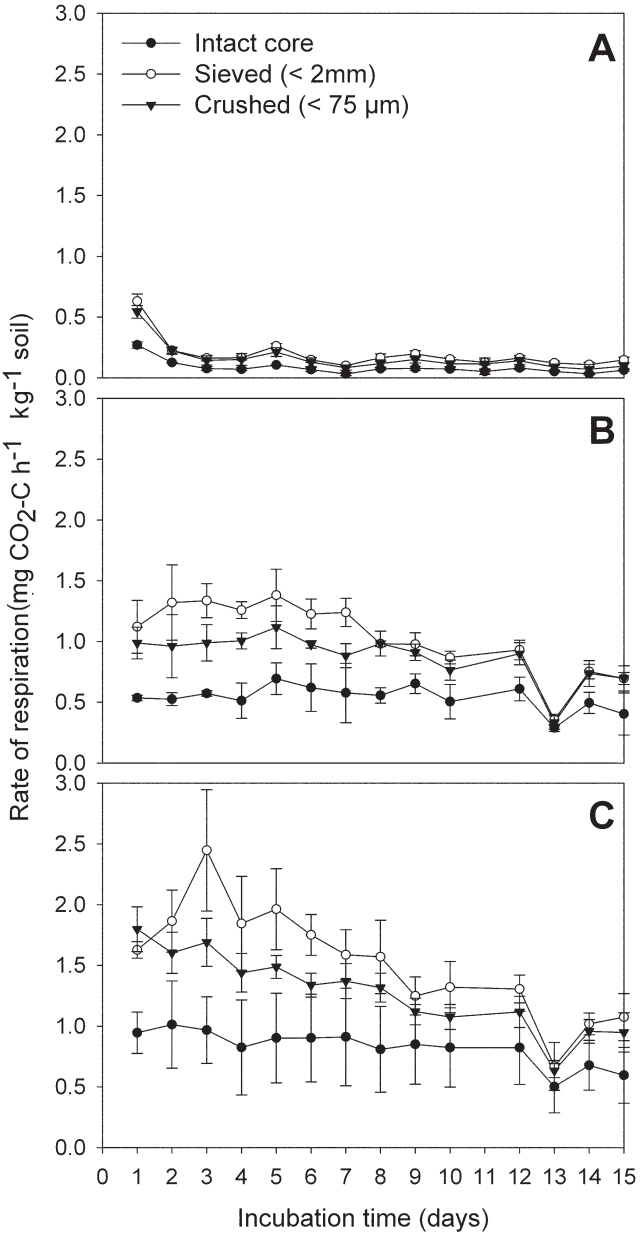

Fig. 1. Rates of soil respiration during incubation of soil core materials at (A) 15°C, (B) 25°C, and (C) 35°C in Exp. 1. Error bars represent standard deviations (*n* = 4).

RESULTS

Respiration rates during the incubation of intact, sieved, and crushed soil (Exp. 1) increased with increasing incubation temperature (Fig. 1). While relatively constant at 15 and 25°C, the rates showed a slight downward trend during incubation at 35°C, suggesting a depletion of labile substrates at this temperature. Similar results were observed in Exp. 2 and 3 with isolated and reconstituted macroaggregates (data not shown). For each of the three incubation experiments, cumulative CO_2 respiration also increased significantly ($P < 0.001$ in each experiment) with increasing incubation temperature (Table 1). The response of cumulative CO_2 respiration to the physical disruption and compartmentalization treatments differed among the experiments (Table 1). Physical disruption treatments ($P < 0.001$) and the interaction with temperature ($P = 0.005$) were significantly different in Exp. 1. In Exp. 2, cumulative CO_2 did not differ between intact and crushed macroaggregates ($P = 0.606$), with a statistically significant interaction ($P = 0.036$). Cumulative CO_2 respiration during Exp. 3 differed significantly between wheat residue amendment treatments ($P = 0.019$), with no statistically significant interaction with temperature ($P = 0.770$). While the overall residue location treatment effect was significant in the ANOVA, pairwise comparisons revealed that the inside vs. outside treatments were not significantly different ($P = 0.335$).

The temperature sensitivity of soil respiration, as expressed by respiration quotients (Q_{10}), was not significantly different among the physical protection treatments in Exp. 1 ($P = 0.874$), was only slightly greater for intact vs. crushed macroaggregates in Exp. 2 ($P = 0.090$), and was not significantly different between the amendment treatments in Exp. 3 ($P = 0.911$) (Table 2).

Microbial biomass C and specific respiration were determined at the end of Exp. 2 to test for a potential cause for increased CO_2 efflux with increased temperature. Microbial biomass C was significantly greater ($P < 0.001$) at 35 than 25°C (Table 3), and was also significantly greater ($P = 0.011$) in intact macroaggregates than crushed macroaggregates (Table 3). The interaction term of the ANOVA was not statistically significant ($P = 0.942$). Specific respiration (kg respired C kg^{-1} microbial biomass C [MBC], Table 3) was significantly greater ($P < 0.001$) after incubation at 25°C (LS mean = 0.637 kg C kg^{-1} MBC) than after incubation at 35°C (LS mean = 0.505 kg C kg^{-1} MBC), but did not differ between physical protection treatments ($P = 0.064$), with no statistically significant interaction ($P = 0.134$).

Table 1. Cumulative CO_2 respiration during incubation of various physical protection treatments at three temperatures (mean ± standard deviation).

Experiment	Treatment	Cumulative CO_2 respiration			
		15°C	25°C	35°C	Mean†
		mg CO_2–C kg^{-1} soil			
1: Soil core material (15 d, *n* = 4)	intact	30.1 ± 3.6	179.3 ± 39.7	295.0 ± 106	168.1
	sieved (<2 mm)	69.0 ± 6.8	368.3 ± 28.1	543.4 ± 53.0	326.9
	crushed (<75 µm)	57.2 ± 10.7	315.6 ± 27.0	442.4 ± 23.4	271.9
2: Isolated macroaggregates (14 d, *n* = 5)	intact (2–4 mm)	147.3 ± 7.2	234.3 ± 8.7	263.6 ± 13.8	215.1
	crushed (<500 µm)	162.8 ± 6.0	237.8 ± 8.8	251.2 ± 18.4	217.3
3: Reconstituted macroaggregates (30 d, *n* = 4)	no amendment	–	921.2 ± 123.9	1224.5 ± 64.1	1073
	amendment inside	–	1059.6 ± 113.5	1430.0 ± 95.4	1245
	amendment outside	–	1015.4 ± 114.2	1315.1 ± 131.3	1165

† Least square mean across temperatures; SE = 14.2 in Exp. 1, 10.1 in Exp. 2, 38.7 in Exp. 3.

Stable isotope signatures of the respired CO_2 were measured in Exp. 3 to determine the relative decomposition of the added substrate. The $\delta^{13}CO_2$ values were significantly greater ($P < 0.001$) at 25 than 35°C (Table 4). Across both incubation temperatures, differences in $\delta^{13}CO_2$ values due to the residue location treatments declined during the experiment. While the $\delta^{13}CO_2$ values for amended vs. unamended samples remained statistically different throughout the experiment, differences between inside vs. outside of macroaggregates were significant only at the first measurement ($P < 0.001$ at Day 2, $P = 0.199$ at Day 9, and $P = 0.766$ at Day 30).

Table 2. Respiration quotients (Q_{10}) for various physical protection treatments incubated separately at two or three temperatures (mean ± standard deviation, $n = 4$ or 5).

Experiment	Treatment	Q_{10}
1: Soil core material	intact cores	2.95 ± 0.45
	sieved cores (<2 mm)	2.81 ± 0.35
	crushed cores (<75 μm)	2.80 ± 0.32
2: Isolated macroaggregates	intact (2–4 mm) macroaggregates	1.34 ± 0.14
	crushed (<500 μm) macroaggregates	1.24 ± 0.18
3: Reconstituted macroaggregates	no amendment	1.34 ± 0.33
	inside macroaggregates	1.35 ± 0.29
	outside macroaggregates	1.30 ± 0.39

DISCUSSION AND CONCLUSIONS

Experimental evidence for the physical protection of SOM in macroaggregates has come from a number of experiments that have shown increased C and N mineralization with crushing, particularly in cultivated soils (as reviewed by Balesdent et al., 2000; Six et al., 2002); however, not all experiments have demonstrated similar results (Franzluebbers, 1999; Garcia-Oliva et al., 2004; Pulleman and Marinissen, 2004; Stenger et al., 2002). We suspect that the physical disruption treatments used in our experiments may have been insufficient to release large amounts of physically protected SOM for decomposition. There is some evidence to suggest that disruption of microaggregates (grinding to <50 μm) rather than macroaggregates (crushing to <250 μm) is required to release SOM and observe an increase in respiration (Six et al., 2002). Conversely, the placement of residues inside of reconstituted macroaggregates should have increased respiration compared with residues placed outside of macroaggregates by reducing the compartmentalization of substrates and decomposers.

The lack of differences in the Q_{10} values among physical disruption treatments does not support our original hypothesis that the largest Q_{10} values would be observed in the treatment with the least physical protection. Soil aggregation is known to reduce the decomposability of otherwise labile material by physically separating the substrate from the microbial biomass and its enzymes (Oades, 1984). Beare et al. (1994) estimated that SOM physically protected in macroaggregates represented only 10 to 20% of the total mineralizable C and only ~1% of total aggregate C. If one also considers microaggregates (by crushing to smaller sizes), physical protection represents a greater proportion of total C, but still less than ~5% (Six et al., 2002). The hypothesized attenuation of temperature sensitivity provided by physical protection may therefore be minor compared with the sensitivity imparted by biochemical thermodynamics as expressed by Arrhenius-type equations.

We also sought to determine a potential cause for the increased CO_2 efflux with increased temperature. An increase in soil respiration due to increased temperature may be attributable to an increase in the size of the microbial biomass respiring at the same rate, or to an increase in specific respiration by an unchanged biomass, or some combination of the two. Our results suggest that increased respiration can be attributed to increased microbial biomass. Microbial biomass C was greater at 35°C than at 25°C and specific respiration was lower, meaning that the microbial populations were less efficient in their use of substrate and respired a greater amount of CO_2 per unit biomass C. While temperature dependence of total soil respiration is well established, much less is known about how that dependence affects different groups of microorganisms. Microbial biomass C and N data alone are clearly insufficient to determine changes in the microbial community composition and activity, and further studies in this area should be supported by community structure analyses as well as substrate utilization efficiency analyses.

We performed three tests of whether compartmentalization of substrate and decomposer through physical protection alters the short-term temperature sensitivity of SOM dynamics. Our three incubations of soil samples with varying degrees of physical disruption or compartmentalization showed no significant differences in Q_{10}. Based on these results, we conclude that physical protection of SOM is insufficient to attenuate the temperature sensitivity of decomposition, which may be driven by Arrhenius-like relationships due to biochemical phenomena. It remains important, however, to further test various nonbiochemical SOM protection mechanisms because even fractionally small changes in temperature sensitivity under changing climate can result in globally significant changes in soil C stocks.

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Table 3. Microbial biomass C (MBC), microbial biomass N (MBN), C/N, and specific respiration (amount of CO_2–C respired per unit of MBC) for intact and crushed macroaggregates after incubation at two temperatures (mean ± standard deviation, $n = 5$).

Treatment	Incubation temperature	MBC	MBN	Microbial C/N	Specific respiration
	°C	mg C kg^{-1} soil	mg N kg^{-1} soil		kg C respired kg^{-1} MBC
Intact 2–4 mm macroaggregates	25	389 ± 35	40 ± 11	10.2 ± 1.9	0.61 ± 0.05
	35	526 ± 20	19 ± 6	29.1 ± 7.6	0.50 ± 0.03
Crushed (<500 μm) macroaggregates	25	356 ± 10	39 ± 6	9.2 ± 1.2	0.67 ± 0.03
	35	495 ± 26	21 ± 6	24.6 ± 5.8	0.51 ± 0.05

Table 4. Isotopic signature of respired CO_2 ($\delta^{13}CO_2$) and proportion of residue-derived respiration during incubation of reconstituted macroaggregates containing ^{13}C-labeled wheat straw (mean ± standard deviation, n = 4).

Treatment	Parameter	25°C			35°C		
		Day 2	Day 9	Day 30	Day 2	Day 9	Day 30
No residue	$\delta^{13}CO_2$	−23.3 ± 2.6	−23.7 ± 0.6	−24.8 ± 0.8	−22.96 ± 0.3	−23.9 ± 0.3	−23.2 ± 0.2
Residue inside macroaggregates	$\delta^{13}CO_2$	274.6 ± 20.6	121.1 ± 7.0	90.2 ± 22.3	226.8 ± 23.5	89.3 ± 4.4	52.9 ± 2.3
	proportion of respiration,%	40.0 ± 2.8	19.4 ± 0.9	15.4 ± 3.0	33.5 ± 3.2	15.2 ± 0.6	10.2 ± 0.3
Residue outside macroaggregates	$\delta^{13}CO_2$	205.5 ± 24.4	118.5 ± 6.7	107.0 ± 30.9	187.9 ± 29.7	66.4 ± 6.6	42.4 ± 6.1
	proportion of respiration, %	30.7 ± 3.3	19.1 ± 0.9	14.1 ± 7.9	28.3 ± 4.0	12.1 ± 0.9	12.7 ± 7.8

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